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Comparison of the vertebrate faunas of the Lower Old Red Sandstone of the Anglo-Welsh Basin with contemporary faunas in Scotland

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ABSTRACT

The Lower Old Red Sandstone terranes of the Midland Valley of Scotland and the Anglo-Welsh Basin have been considered as separate realms due to the rarity of fish species common to both areas. Although in the first half of the 19th century the osteostracan *Cephalaspis lyelli* was thought to occur in both terranes this was shown in be incorrect in the latter part of that century. It was not until 1968 that it was demonstrated that the thelodont agnathan *Turinia pagei* occurred in both terranes. This species has a much wider distribution across the whole of the Old Red Sandstone continent, but its presence in both realms indicates they were connected either directly or indirectly. In 2012 it was suggested that the osteostracan *Janaspis watsoni* might be present in both basins and in 2013 the acanthodian *Parexus recurvus* was shown to definitely occur in both. Here we show that other acanthodian genera and species were present in both regions during the Lochkovian (earliest Devonian). Co-specific plants also occur in both terranes during the Lochkovian. As there is no evidence of a marine connection to the Midland Valley in the Lochkovian, the only logical conclusion is that the connection between the two terranes was fluvial.

1. Introduction

The Lower Old Red Sandstone consists of a large suite of sedimentary rocks that were laid down in the Middle Silurian to Early Devonian. In the Midland Valley Terrane, the rocks are predominantly alluvial deposits influenced by significant igneous activity. Due to the sediments being mostly non-marine they are generally fossil poor, although at certain localities very rich accumulations of fossil fish are found. In Scotland the Lower Old Red Sandstone spans the Wenlock-Ludlow to the Emsian. The fish-bearing horizons are Wenlock-Ludlow to Lochkovian in age and are found mostly within the Midland Valley Terrane. The depositional history of the Midland Valley is very complicated and we refer to Browne and Barclay (2005) and references therein for details. In the Anglo-Welsh Basin the Lower Old Red Sandstone also spans the Wenlock-Ludlow to the Emsian with the fish bearing horizons mostly extending from the Přídolí to Pragian. Like the Midland Valley the sedimentation is very complex (see Barclay, 2005a and references therein). Comparison between the stratigraphic occurrences of taxa in the two regions is hampered by older literature and museum collection labels using local stage names and colloquial appellations for the Anglo-Welsh Basin strata rather than the international standard. For the purposes of this paper, the Downtonian is considered equivalent to the Přídolí, and the Dittonian is equivalent to the Lochkovian. Fig. 1 illustrates the relationship and stratigraphy between the Old Red Sandstone of Scotland and the Anglo-Welsh Basin in a simplified form. For more detailed figures of all the various geological subdivisions in the Anglo-Welsh Basin we refer to Allen (1977, Fig. 7) and Dineley (1999a, Fig. 4.2).

Institutional abbreviations—FMNH: Field Museum of Natural History, Chicago, USA; GSM: British Geological Survey, Keyworth, United Kingdom; NHM: Natural History Museum, London, United Kingdom; NMS: National Museums of Scotland, Edinburgh, United Kingdom; OUMNH: Oxford University Museum of Natural History.

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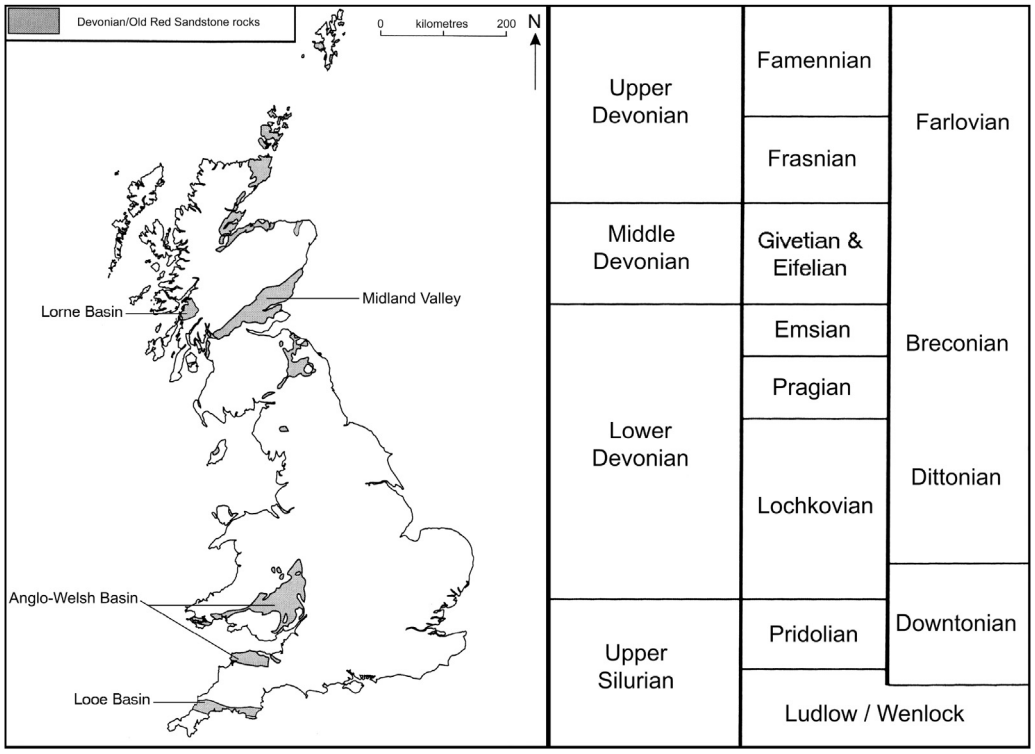

Fig. 1. Map and stratigraphical column of Old Red Sandstone of Great Britain. Map modified from Barclay (2005b, Fig. 1.1). Stratigraphical column modified from Love and Williams (2000, Fig. 2).

2. Historical background to the Scottish Lower Old Red Sandstone fish assemblages

The majority of Lower Old Red Sandstone fish are found in the Midland Valley Terrane of Scotland (but see Lorne Basin fauna below), which is generally considered to lie between the Highland Boundary Fault and the Southern Uplands Fault. The lowest fish-bearing stratum is the Wenlock-Ludlow Cowie Harbour Fish Bed, described in detail by Dineley (1999b). Well-preserved agnathan remains are present, including the osteostracan *Hemiteleaspis heintzi* Westoll, 1945, the anaspid *Cowielepis ritchiei* Blom, 2008 and the heterostracan *Traquairaspis campbelli* (Traquair, 1912). As none of the genera are found in the Anglo Welsh Basin they will not be discussed further in this work.

Most fish-bearing outcrops are found in the Lochkovian strata between the Highland Boundary Fault and Southern Uplands Fault. The first species to be described was the cephalaspid *Cephalaspis lyelli* Agassiz, 1835. Many new specimens of "*Cephalaspis*" were found in numerous quarries and natural outcrops but they were first formally described by Lankester (1870, Fig. 2A). Other "*Cephalaspis*" species were erected later, particularly by Stensiö (1932) and White (1963). The first heterostracan was described although not named by Mitchell (1862). It was Powrie (Fig. 2B) who formally described this species as *Pteraspis mitchelli* Powrie, 1864a in honour of Mitchell (Fig. 2C). The only thelodont species discovered to date is *Turinia pagei* (Powrie, 1870). This was the first articulated and relatively complete thelodont to be described.

Jawed fish remains comprising isolated acanthodian fin spines from Balruddery Den were first mentioned by Miller (1841). It was Agassiz (1844–1845) who formally described and figured these remains, erecting two species *Climatius reticulatus* Agassiz, 1844 and *Parexus recurvus* Agassiz, 1844. In the posthumous edition of Hugh Miller's Old Red Sandstone is a sketch (Miller, 1858, p. 160) of two unnamed acanthodian fin spines from Balruddery Den. The upper fin spine is similar to the pectoral spines of *Vernicomacanthus uncinatus* (Powrie, 1864b ex Egerton MS), a genus supposedly found in the Anglo-Welsh Basin (Miles, 1973). The first articulated acanthodians were described by Egerton (1861) (Fig. 2D); the specimens are from Farnell. However it was Powrie (1864b, 1870) who contributed the greatest advancement in knowledge of the articulated fishes in the early days. Davidson and Newman (2003) provided a brief biography and resumé of Powrie's work. For a comprehensive list of the fish fauna see Dineley (1999c).

For completeness it is worth mentioning isolated Lower Old Red Sandstone fish-bearing outcrops north of the Highland Boundary Fault in the Lorne Basin (Fig. 1). This area (which includes the island of Kerrera) has yielded the cephalaspid *Cephalaspis lornensis* Traquair, 1899 (this species probably does not belong in *Cephalaspis* as Sansom (2009) does not include this species in the genus), *Gylenaspis maceacheni nomen nudum* Tarlo and Gurr, 1964 and the anaspid *Kerreralepis carinata* Blom, 2012. The fauna including some fragmentary remains, but no acanthodians other than a solitary, poorly preserved *Mesacanthus*, was recently described by Trewin et al. (2012) in more detail. Trewin et al. (2012) concluded, based on the fauna and flora (including palynology), that the deposits were near the Siluro-Devonian boundary, probably lowermost Devonian. However, as none of the genera can reliably be said to occur in the Anglo-Welsh Basin we will not discuss it further.

3. Historical background to the Anglo-Welsh Basin Lower Old Red Sandstone fish assemblages

The Lower Old Red Sandstone of the Anglo-Welsh Basin extends from Pembrokeshire to Gloucestershire with outliers in Somerset and north Devon. The first fish species were described by Agassiz who erected three species (*Cephalaspis rostratus*,*Cephalaspis lewisii* and *Cephalaspis lloydii*) all now synonymised under *Pteraspis rostratus* (Agassiz, 1835), a heterostracan. Also, some of Agassiz' specimens of the osteostracan *C. lyelli* (Agassiz, 1835, vol. 2, pl. 1b,

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